

A NEW EXOCRINE GLAND IN THE SLAVE RAIDING ANT GENUS *POLYERGUS*

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INTRODUCTION

In his classical study of the workers and males of *Myrmica rubra*, Janet (1898, 1901) discovered a pair of clusters of a few glandular cells under the 6th abdominal tergite. Each cell is drained by a duct that penetrates the intersegmental membrane between the 6th and 7th abdominal tergites. Recent investigations have demonstrated that this gland is very common in ants, but it varies considerably in size and structure (Hölldobler and Engel 1978). Since the gland is anatomically closely associated with the last exposed tergite in female ants (7th abdominal tergite = pygidium) Kugler (1978) suggested that it be called the *pygidial gland*. Recently Jessen and Maschwitz (1983) proposed the alternative name, *Janet's gland*, in honor of its discoverer Charles Janet.

The pygidial gland has been found in workers of representative species belonging to all subfamilies except the Formicinae (for literature review see Hölldobler and Engel 1978; Hölldobler and Engel-Siegel 1982; Hölldobler 1982).

I report here the first discovery of a pygidial gland in *Polyergus*, a genus of the subfamily Formicinae. But the anatomy has unusual features that point to a possibly independent origin in evolution.

MATERIAL AND METHODS

Three species of *Polyergus* were investigated. The European species *Polyergus rufescens* was collected near Würzburg (W-Germany), the two North American species *P. breviceps* and *P. lucidus* were found near Portal (Arizona) and near Rocky Point in Suffolk County (New York), respectively. Virgin queens and males were

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available only in the case of *P. lucidus*. For comparison two common slave species of *P. rufescens*, *Formica rufibarbis* and *F. fusca* (from the Würzburg area), as well as two species of the slave raiding *Formica sanguinea* group (collected in Massachusetts), were also studied.

For histological investigations life specimens were fixed in alcoholic Bouin or Carnoy (Romeis 1948), embedded in methylmethacrylate, and sectioned 6–8 μ thick with a D-profile steel knife on a Jung Tetrander I microtome (Rathmayer 1962). The staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A scanning electron microscope.

RESULTS

Workers and queens of the three *Polyergus* species investigated possess a large, tergal complex gland. One part of it is located between the 6th and 7th abdominal tergites; the other part belongs to the 7th tergite (Fig. 1). Because of its anatomical location I propose tentatively to call this organ pygidial gland, although it differs in several respects from the pygidial glands found in other ant subfamilies.

The pygidial gland of *Polyergus* consists of a reservoir, formed by an invagination of the intersegmental membrane between 6th and 7th abdominal tergites. Glandular cells (~80 cells in *P. rufescens* workers) are drained into this reservoir through ducts penetrating the intersegmental membrane. Ducts of a second group of glandular cells open into a series of cuticular cups located along the anterior margin of the 7th abdominal tergite (Fig. 1, 2). This striking cuticular structure is usually not visible, because it is covered by the posterior portion of the 6th abdominal tergite. It is, however, easily exposed by slightly pulling the two terminal abdominal tergites apart. Although only a few specimens of each species were investigated in detail, species-specific differences in the pygidial cup structure are so conspicuous that this organ might be considered a valid taxonomic character.

The cup structure is most strikingly developed in workers of *P. rufescens* (Fig. 2). In this case several cups are often merged to form one large cup containing 2–5 glandular cell openings. I counted a total of approximately 250 duct openings on the pygidium of *P. rufescens* workers. In workers of *P. breviceps* the cup structure is

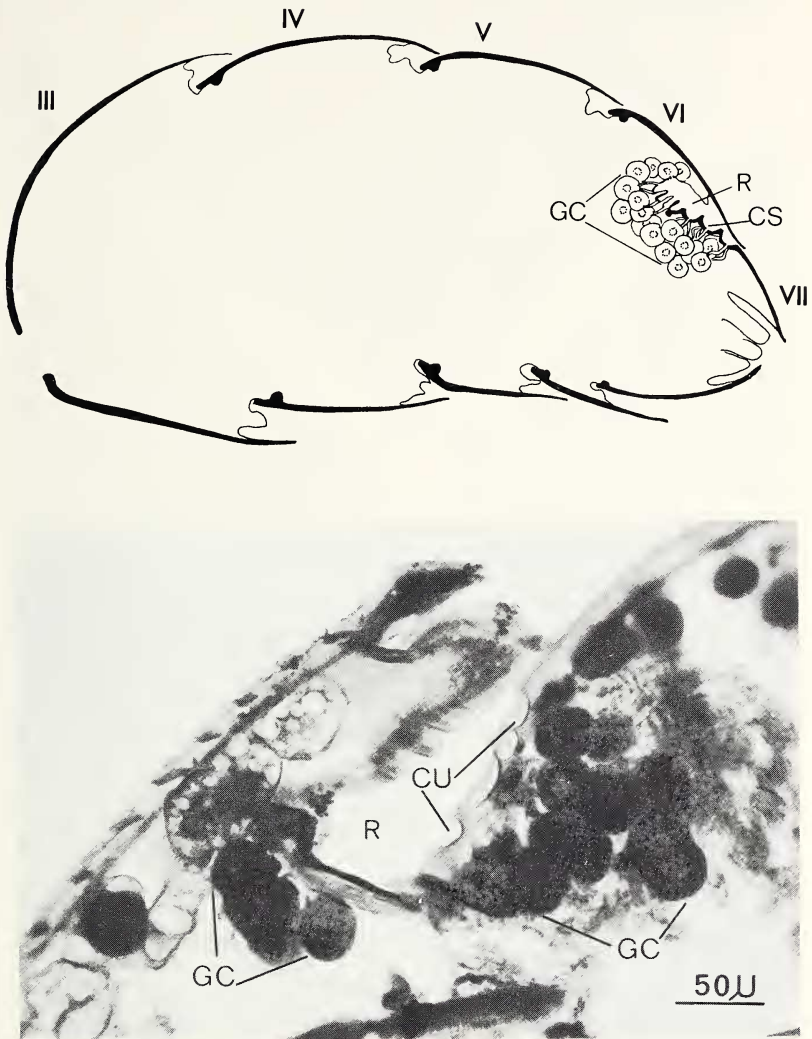


Fig. 1. Above: Schematic illustration of the *Polyergus* pygidial gland between 6th and 7th abdominal tergites. Below: Longitudinal section through the pygidial gland of a *P. rufescens* worker. CS: cup structure; CU: cup; GC: glandular cells; R: intersegmental reservoir.

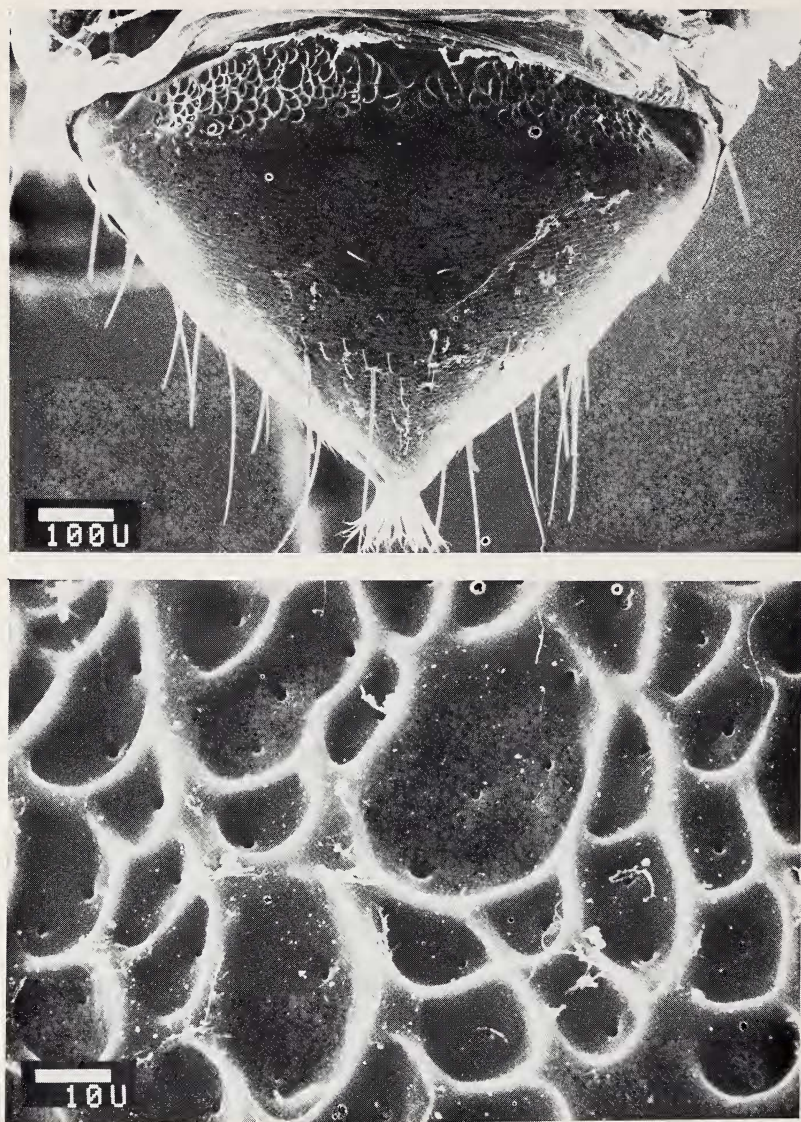


Fig. 2. SEM-photographs of the pygidial cup structure of a *P. rufescens* worker. Above: overview of the pygidium (= 7th abdominal tergite). Below: close-up of the cup structure. Note the duct openings inside the cups.

smaller (with a total of ~150 duct openings), but in this species as well several small cups frequently form one large cup (Fig. 3). In *P. lucidus* workers the pygidial cup structure is still smaller, with approximately 100 duct openings. In this case the cup structure consists primarily of single cups (Fig. 4). It is interesting to note, however, that in *P. lucidus* queens the pygidial cup structure is considerably larger (~200 duct openings), and many of the cups are merged (Fig. 5).

External morphological studies of *P. lucidus* males indicate that they lack the organ.

Formica rufibarbis and *F. fusca*, two common slave species of *P. rufescens*, as well as two representatives of the slave raiding *Formica sanguinea* group were found not to possess a pygidial gland (Fig. 6).

DISCUSSION

Of a total of 17 formicine species investigated (the current study and Hölldobler and Engel 1978) belonging to 6 genera (*Acantholepis*, *Camponotus*, *Formica*, *Myrmecocystus*, *Oecophylla*, *Polyergus*) only those in *Polyergus* possess the pygidial gland. This structure is a complex gland with one group of glandular cells opening into an intersegmental reservoir, and another group of cells being drained into cuticular cups in the 7th abdominal tergite. From these features and from its general anatomy I conclude that the pygidial gland of *Polyergus* is not homologous with the pygidial gland of other ant subfamilies, but has evolved independently, possibly in connection with the highly specialized slave raiding behavior of *Polyergus*.

Polyergus slave raids are organized by scout ants that deposit chemical trails (Talbot 1967). The precise origin of the trail pheromones has not yet been established. In most formicine species secretions from the rectal bladder serve as trail pheromones (for review see Hölldobler 1978). These function in many cases primarily as orientation cues and are often supplemented by excitement (or arousal) signals, which can be chemical or mechanical in nature. Recent observations suggest that recruitment to slave raids in *Polyergus* might be based on a similar mechanism.

Topoff et al. (1984) found that individual scout ants lead the raiding party of nestmates to the slave ants' nest. He observed that the ants, although following a chemical trail, tend to "swarm"

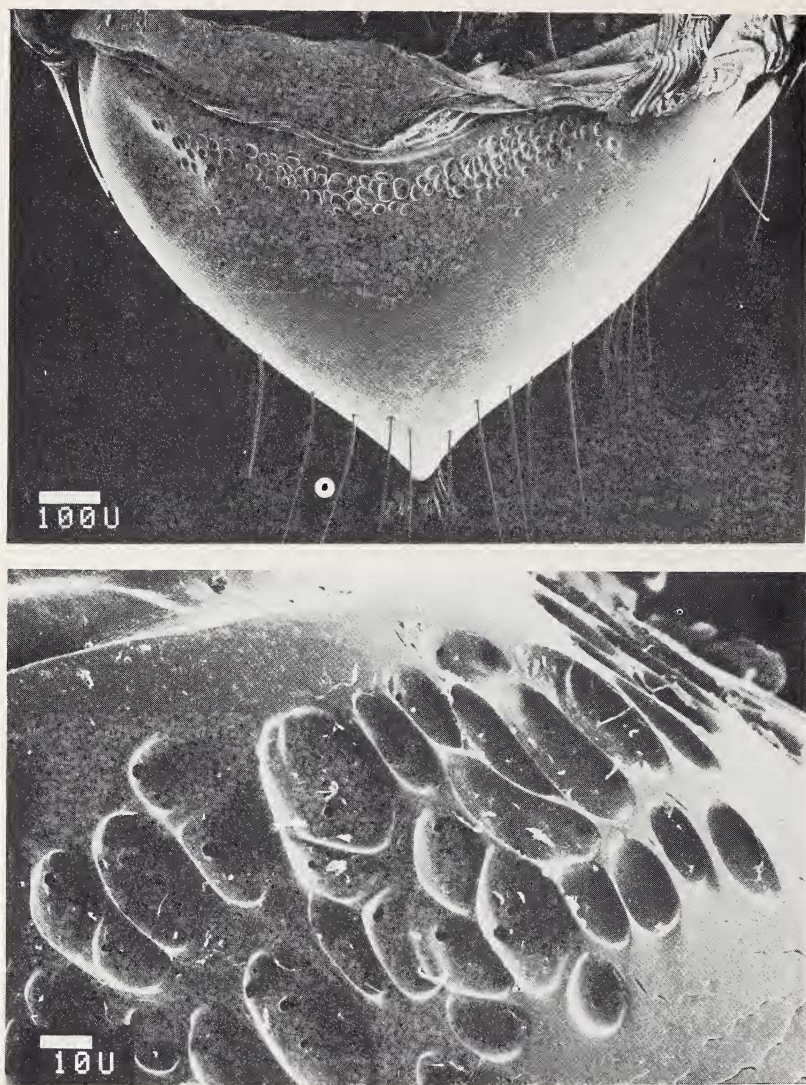


Fig. 3. SEM-photograph of the pygidial cup structure of a *P. breviceps* worker. Above: overview of the pygidium. Below: close-up of the cup structure.

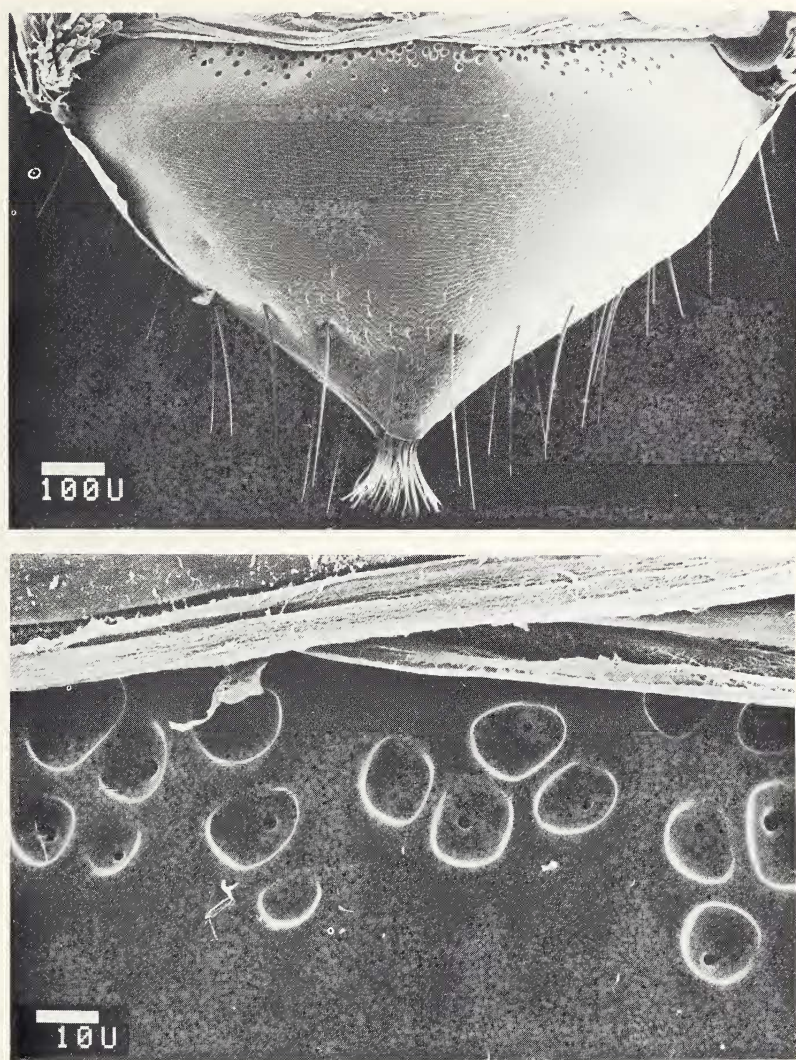


Fig. 4. SEM-photograph of the pygidial cup structure of a *P. lucidus* worker. Above: overview of the pygidium. Below: close-up of cup structure.

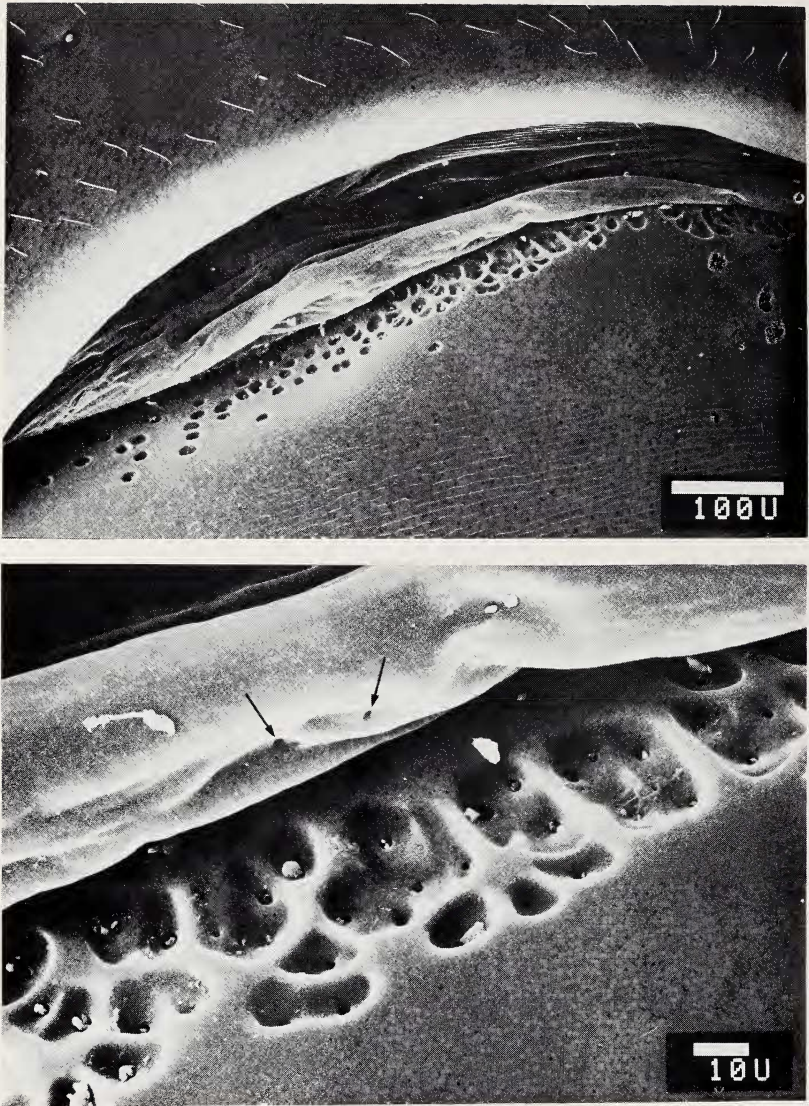


Fig. 5. SEM-photograph of the pygidial cup structure of a *P. lucidus* queen. Above: overview of the cup structure at the anterior margin of the 7th abdominal tergite. Below: close-up of the cup structure. Arrows point at the intersegmental duct openings.

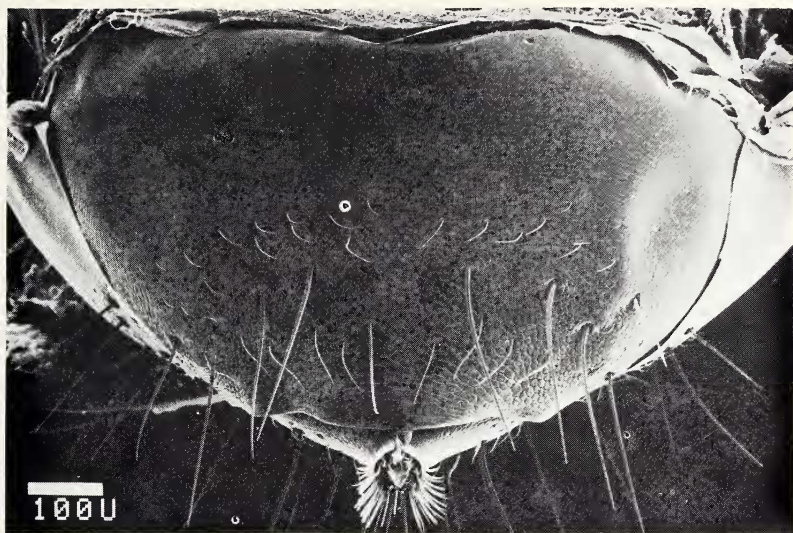


Fig. 6. SEM-photograph of the pygidium of a worker belonging to the *Formica sanguinea* group. Note: no cup structure on the anterior margin of the 7th abdominal tergite.

around the leader ant, often moving briefly ahead, but always returning to the leader. Myrmecologists have long noted this peculiar looping behavior at the front of the raiding columns of *Polyergus* (see for example Schmitz 1906), but only the recent studies by Topoff have indicated that this appears to be due to the organizing role and excitement emanating from the leader ant. These observations suggest that the leader discharges not only a longer lasting trail pheromone but also an arousal signal, possibly from the pygidial gland.

Similar recruitment patterns have been observed in *Camponotus socius* and *Myrmecocystus mimicus*, where secretions from the poison gland seem to function as arousal signals (Hölldobler 1971, 1981), as well as in *Camponotus ephippium*, where the arousal signal appears to originate from the cloacal gland (Hölldobler 1982).

However, this hypothesis cannot be applied to the well developed pygidial gland in *Polyergus* queens. Wasmann (1915) first proposed that a young *Polyergus* queen, in order to found a new colony, has to intrude a colony of a slave ant species, where she kills the resident

queen and is subsequently adopted as the "replacement" queen by the slave ant workers. This mode of parasitic colony founding was later confirmed in field observations by Gösswald (1932).

It is possible that the *Polyergus* queen achieves her acceptance in the foreign colony by emitting either a supernormal attractant or a disorganizing alarm substance (hence, some form of queen "propaganda" substance), possibly discharged from the pygidial gland. In fact, the pygidial gland secretions of *Polyergus* workers might also function as a kind of propaganda allomone when encountered by slave ants, very similar to the Dufour's gland secretions of the slave raiding species *Formica pergandei* and *Formica subintegra* which have a confusing propaganda effect on the raided slave ant colony (Regnier and Wilson 1971).

Further experimental work is required to determine which, if any, of these proposed speculations on the function of the *Polyergus* pygidial gland is correct.

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REFERENCES

- GÖSSWALD, K.
1932. Ökologische Studien über die Ameisenfauna des mittleren Maingebietes. Zeitschrift f. Wissensch. Zoologie **142**: 1-156.
- HÖLLDOBLER, B.
1971. Recruitment behavior in *Camponotus socius* (Formicidae). Z. vergl. Physiol. **75**: 123-142.
- HÖLLDOBLER, B.
1978. Ethological aspects of chemical communication in ants. Advances in the Study of Behavior. **8**: 75-115.
- HÖLLDOBLER, B.
1981. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. **9**: 301-314.
- HÖLLDOBLER, B.
1982a. Chemical communication in ants: new exocrine glands and their behavioral function. In: The Biology of Social Insects (ed. M. Breed, C. D. Michener, H. E. Evans). Westview Press, Boulder, Colorado.

HÖLLDOBLER, B.

- 1982b. The cloacal gland, a new pheromone gland in ants. *Naturwissenschaften* **69**: 186.

HÖLLDOBLER, B. AND H. ENGEL

1978. Tergal and sternal glands in ants. *Psyche* (Cambridge) **85**: 285–330.

HÖLLDOBLER, B. AND H. ENGEL-SIEGEL

1982. Tergal and sternal glands in male ants. *Psyche* (Cambridge) **89**: 113–132.

JANET, CH.

1898. Etudes sur les Fourmis, les Guêpes et les Abeilles, Note 17: Systeme glandulaire tégumentaire de la *Myrmica rubra*. Observations diverses sur les Fourmis. Paris. Georges Carré et C. Naud, Éditeurs pp. 1–30.

JANET, CH.

1902. Anatomie du gaster de la *Myrmica rubra*. Paris, Georges Carré et C. Naud, Éditeurs pp. 1–63.

JESSEN, K. AND U. MASCHWITZ

1983. Abdominaldrüsen bei *Pachycondyla tridentata* (Smith) (Formicidae, Ponerinae). *Insectes Sociaux* **30**: 123–133.

KUGLER, CH.

1978. Pygidial glands in myrmicine ants (Hymenoptera, Formicidae). *Insectes Sociaux* **25**: 267–274.

RATHMAYER, W.

1962. Methylmetacrylat als Einbettungsmedium für Insekten. *Experientia* (Basel) **18**: 47–48.

REGNIER, F. E. AND E. O. WILSON

1971. Chemical communication and “propaganda” in slave maker ants. *Science* **172**: 267–269.

ROMEIS, B.

1948. *Mikroskopische Technik*. München 1948.

SCHMITZ, H.

1906. Das Leben der Ameisen und ihrer Gäste. Verlagsanstalt vorm. G. J. Manz, Buch- u. Kunstdruckerei, München-Regensburg.

TALBOT, M.

1967. Slave raids of the ant *Polyergus lucidus* Mayr. *Psyche* (Cambridge) **74**: 299–313.

TOPOFF, H., B. LAMON, L. GOODLOE, AND M. GOLDSTEIN

1984. Social and orientation behavior of *Polyergus breviceps* during slave-making raids. *Behav. Ecol. Sociobiol.* **15**: 273–279.

WASMANN, E.

1915. *Gesellschaftsleben der Ameisen*, Münster, 1915.